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Abstract: Population dynamics are the result of an interplay between extrinsic and intrinsic environmental drivers. Predicting the effects of environmental change on wildlife populations therefore requires a thorough understanding of the mechanisms through which different environmental drivers interact to generate changes in population size and structure. In this study, we disentangled the roles of temperature, food availability and population density in shaping short- and long-term population dynamics of the African striped mouse, a small rodent inhabiting a semidesert with high intra- and interannual variation in environmental conditions. We parameterized a female-only stage-structured matrix population model with vital rates depending on temperature, food availability and population density, using monthly mark–recapture data from 1609 mice trapped over 9 years (2005–2014). We then applied perturbation analyses to determine relative strengths and demographic pathways of these drivers in affecting population dynamics. Furthermore, we used stochastic population projections to gain insights into how three different climate change scenarios might affect size, structure and persistence of this population. We identified food availability, acting through reproduction, as the main driver of changes in both short- and long-term population dynamics. This mechanism was mediated by strong density feedbacks, which stabilized the population after high peaks and allowed it to recover from detrimental crashes. Density dependence thus buffered the population against environmental change, and even adverse climate change scenarios were predicted to have little effect on population persistence (extinction risk over 100 years <5%) despite leading to overall lower abundances. Explicitly linking environment–demography relationships to population dynamics allowed us to accurately capture past population dynamics. It further enabled establishing the roles and relative importances of extrinsic and intrinsic environmental drivers, and we conclude that doing this is essential when investigating impacts of climate change on wildlife populations.

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Density feedbacks mediate effects of environmental change on population dynamics of a semi-desert rodent

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Abstract

1. Population dynamics are the result of an interplay between extrinsic and intrinsic environmental drivers. Predicting the effects of environmental change on wildlife populations therefore requires a thorough understanding of the mechanisms through which different environmental drivers interact to generate changes in population size and structure.

2. In this study, we disentangled the roles of temperature, food availability, and population density in shaping short- and long-term population dynamics of the African striped mouse, a small rodent inhabiting a semi-desert with high intra- and inter-annual variation in environmental conditions.

3. We parameterized a female-only stage-structured matrix population model with vital rates depending on temperature, food availability, and population density, using monthly mark-recapture data from 1609 mice trapped over 9 years (2005-2014). We then applied perturbation analyses to determine relative strengths and demographic pathways of these drivers in affecting population dynamics. Furthermore, we used stochastic population projections to gain insights into how three different climate change scenarios might affect size, structure, and persistence of this population.

4. We identified food availability, acting through reproduction, as the main driver of changes in both short- and long-term population dynamics. This mechanism was mediated by strong density feedbacks, which stabilized the population after high peaks and allowed it to recover from detrimental crashes. Density dependence thus buffered the population against environmental change,

and even adverse climate change scenarios were predicted to have little effect on population persistence (extinction risk over 100 years $< 5\%$) despite leading to overall lower abundances.

5. Explicitly linking environment-demography relationships to population dynamics allowed us to accurately capture past population dynamics. It further enabled establishing the roles and relative importances of extrinsic and intrinsic environmental drivers, and we conclude that doing this is essential when investigating impacts of climate change on wildlife populations.

Keywords

environmental drivers, environmental stochasticity, extrinsic, intrinsic, LTRE, matrix model, perturbation analysis, population dynamics, rodent, vital rate

Introduction

Contemporary climate change happens at a fast rate, and increases in temperatures and the frequency of extreme events are predicted to continue (IPCC, 2014). Effects of climate change on ecological systems have already become evident (Parmesan, 2006) and manifest themselves as alterations in species distributions (Chen *et al.*, 2011), shifts in phenology (Charmantier *et al.*, 2008), and changes in abundance (Pounds *et al.*, 2006; Jepsen *et al.*, 2008). These impacts make it more important than ever to understand and predict how climate affects life-history processes and population dynamics of animals and plants both directly and indirectly (*e.g.*

through resource availability)(Williams *et al.*, 2002).

Population dynamics are the result of an interplay between different extrinsic and intrinsic environmental factors (Stenseth *et al.*, 2002; Goswami *et al.*, 2011). Extrinsic factors such as climate and resource availability interact with intrinsic density feedbacks to generate variation in vital rates (survival, reproduction). Vital rate variation then translates into changes in population size and structure (Leirs *et al.*, 1997; Lima *et al.*, 1999). The impacts of extrinsic environmental factors and how these are affected by density may differ among seasons (*e.g.* Gullett *et al.*, 2014), across species' life cycles (Gamelon *et al.*, 2017) and be subject to stochastic variation among years, making population dynamics dependent not only on current, but also on past conditions (Wilmers *et al.*, 2007). Predicting potential impacts of climate change on species and ecosystems therefore requires an in-depth understanding of how deterministic and stochastic variation in climate, resource availability, and density feedbacks jointly affect population dynamics (Benton *et al.*, 2006; Boyce *et al.*, 2006). Such understanding can be gained through quantitative models that explicitly link environmental factors to population dynamics via vital rates (Ehrlén *et al.*, 2016) and the availability of long-term individual-based data necessary to parameterize these models (Clutton-Brock & Sheldon, 2010).

Collecting sufficient amounts of long-term individual-based data is easier for species with short generation time, such as rodents. Rodent life histories are also of particular interest because they are highly sensitive to the environment, and consequently show large numerical fluctuations within and among years (Krebs, 2013). These fluctuations are of great ecological, social, and economical interest. They are, for example, linked to ecosystem consequences of the dampening of vole

and lemming population cycles (Ims *et al.*, 2008; Schmidt *et al.*, 2012), stochastic rodent eruptions with detrimental effects on crop production (Singleton *et al.*, 2010), and high risks of disease outbreaks (Gubler *et al.*, 2001). Rodents are also often keystone species in food-webs and can function as ecosystem engineers (Kelt, 2011). Furthermore, while studying rodent populations - particularly in the context of environmental change - is worthwhile in itself, drivers and mechanisms of population dynamics may also be conserved across species. From a broader perspective, we may thus be able to use studies on easily accessible rodent systems to gain valuable insights into general principles of population dynamics in variable environments and to draw inferences about related or ecologically similar species for which long-term individual-based data are not available (Frederiksen *et al.*, 2014).

Here, we study population dynamics of the African striped mouse (*Rhabdomys pumilio*), a small rodent inhabiting a semi-arid ecosystem characterized by considerable variation in timing and amount of annual rainfall and, consequently, availability of green vegetation (Cowling *et al.*, 1999). Being adapted to such a variable environment, the species displays high degrees of phenotypic plasticity (Raynaud & Schradin, 2008; Nel *et al.*, 2015) and potentially large adaptive capacity in the face of environmental change (Rymer *et al.*, 2013). Variation in vital rates of this rodent has previously been linked to temperature, food availability, and population density (Nater *et al.*, 2016a). In this study, we re-analyse these environment-demography relationships and link them to population dynamics in a stage-structured population model. We then subject this model to retrospective perturbation analysis to identify the roles and relative strengths of environmental drivers in generating past population dynamics, and to prospective perturbation

analysis to investigate potential future responses of the African striped mouse to alterations in the stochastic environment including different scenarios for future climate change.

Materials and methods

STUDY SYSTEM AND DEMOGRAPHIC DATA

The African striped mouse (*Rhabdomys pumilio*) is a small murid rodent (adult body mass of 30-85 g in the field) native to the dry regions of South Africa (Mallarino *et al.*, 2018). It is diurnal, forages alone but returns to a nest shared with an extended family group at night (Schradin & Pillay, 2004). Group members share one territory and interact amicably with each other, but are highly aggressive towards striped mice from other groups (Schradin & Pillay, 2004). Striped mice are omnivores, feeding primarily on the leaves of shrubs, small succulents and ephemerals, but have also been observed to eat seeds and insects (Schradin, 2005). Home range sizes vary strongly depending on local population density and seasonal food availability (Schradin, 2006). The main breeding season is in the austral spring. Most striped mice are therefore born between July and November, and can reach sexual maturity after four weeks of age (Schradin & Pillay, 2014). However, they often delay reproduction and remain in their natal territory until the breeding season of the following year and few mice survive to a another breeding season after that (life expectancy rarely exceeds 2 years, Schradin *et al.* (2012)).

The study population of African striped mice is located in the Goegap Nature Reserve in the Succulent Karoo of South Africa (29°41′ S, 18°01′ E; altitude 912 m), a semi-arid winter-rainfall ecosystem with marked vegetation peaks in spring. The

study population has been monitored since 2004 with a monthly capture-mark-recapture program (trapping protocol described in detail in Schradin (2006)). For this study, we assigned female striped mice to one of three life stages based on age and reproductive status. Individuals below the age of four weeks were considered immatures, while those that were older than four weeks but had not yet shown signs of reproduction were assumed to be philopatrics (pre-reproductive adults). Striped mice displaying a perforated vagina in month t-1, and/or signs of lactation in month t were considered breeders (reproductive adults) from month t onwards (Figure 1).

ENVIRONMENTAL DATA

To investigate environmental effects on vital rates and population dynamics of striped mice, we explicitly included ambient temperature, food availability, and adult population density into our analyses.

Monthly mean temperature represents a key seasonal cue, and was calculated by averaging over daily measurements of minimum and maximum temperatures collected at the field station. Absolute minimum and maximum temperatures in each month were highly correlated with monthly mean temperatures (Pearson's r = 0.784 and 0.868 respectively), and were therefore not considered separately in our analyses.

We quantified monthly food availability using estimated abundance of annual succulents and ephemerals eaten by striped mice (34 species, Schradin (2006)). These plants vary seasonally in abundance and are the main driver of both changes in metabolic rates (Rimbach *et al.*, 2018) and reproduction (Nel *et al.*, 2015) of striped mice. We estimated plant abundance based on a vegetation survey within

the study site. Eight monitoring plots (2 x 2 m each) were sampled monthly using a standard protocol (Braun-Blanquet method, Werger (1974)) to determine the amount of ground covered by different species of annual succulents and ephemerals. Monthly food availability was then calculated as the plot-average percentage of ground covered by all plant species. We left out the shrub components of striped mouse diet, *Lycium cinereum* and *Zygophyllum retrofractum*, as the former has annual leaves that covary seasonally with the abundance of annual succulents and ephemerals, while the latter is a succulent that varies little within years and represents an "emergency food" for striped mice when nothing else is available (Schradin, 2006). We also did not consider rainfall directly as a covariate as studies have shown that water is not a limiting resource for striped mice (likely due to being available year-round in succulent shrubs, Schoepf *et al.* (2017)), and precipitation thus affects them primarily through the availability of annual food plants.

Density regulation is a key component in population dynamics of small mammals (Krebs, 2013), and we calculated a proxy for monthly population density by dividing the number of trapped mice by the study area size. We only included adult female mice in the measure, as immature individuals do not compete significantly for reproduction or food. Males were excluded to allow implementing density feedback in the population model without having to make assumptions about sex ratio in family groups and number of male floaters. Further, competition within sexes can be much more important than between sexes (Wauters *et al.*, 2004). This modelling decision was unproblematic as vital rate model selection and matrix model predictions were not sensitive to inclusion of the males in the density measure (results not shown). As a measure for population density was required as a covariate for the mark-recapture model, it was not possible to correct the counts

of trapped mice with recapture probabilities at that stage. However, due to overall high and invariable recapture probabilities over the study period, the raw counts are representative of the total population size (Nater *et al.*, 2016a). The size of the study site varied throughout the study period due to changes in the size of individual home ranges (Schradin *et al.*, 2010), and we estimated it using a 100% minimum convex polygon (MCP) approach (Worton, 1987) on the coordinates of the sampled nests in each month.

ADAPTATION OF VITAL RATE ESTIMATION

In a previous study (Nater *et al.*, 2016a) we had estimated several monthly vital rates of female striped mice as functions of ambient temperature, food availability, and population density for the period from January 2005 to September 2014. Specifically, we had used (1) a multi-state mark recapture model (Lebreton *et al.*, 2009) to estimate monthly survival and maturation probabilities of immatures (S_i, Ψ_{ib}) and philopatrics (S_p, Ψ_{pb}), and survival probability of breeders (S_b), (2) a generalized linear mixed model (GLMM) to estimate the breeding probability (B) of breeders and (3) GLMs to estimate litter probability (L) and litter size (F). For using the vital rate - environment relationships in a matrix population model in this study, we re-defined the breeder stage to accommodate a pure post-breeding census and elevated litter size using auxiliary data to obtain population projections that did not go extinct within a few months. These adaptations and the resulting re-analyses of vital rate - environment relationships are detailed in Appendix 1.

STAGE-STRUCTURED POPULATION MODEL

We used the re-estimated vital rate - environment relationships to build a stage-structured population model for the female segment of the striped mouse population. We defined population structure at time t (N(t)) as a vector containing the number of immatures ($N_i(t)$), philopatrics ($N_p(t)$) and breeders ($N_b(t)$):

$$N(t) = \begin{bmatrix} N_i(t) \\ N_p(t) \\ N_b(t) \end{bmatrix}$$

We then defined transition matrices A(t) (for more information see Caswell, 2001) that describe the monthly transitions between these stages depending on the vital rates in striped mouse life cycle (Figure 1). As all vital rates were functions of monthly temperature, food availability, and population density, the matrix itself was dependent on these environmental covariates (indicated by time-dependence of A):

$$A(t) = \begin{bmatrix} S_i\Psi_{ib}LF & S_p\Psi_{pb}LF & S_bBLF \\ S_i(1-\Psi_{ib}) & S_p(1-\Psi_{pb}) & 0 \\ S_i\Psi_{ib} & S_p\Psi_{pb} & S_b \end{bmatrix}$$

This allowed projecting population size and structure from a given month t to the next $(t+1)$ using $N(t+1) = A(t)N(t)$.

We assessed the ability of the matrix model to capture striped mouse population dynamics by comparing model-generated population hindcasts to the observed

population sizes over the course of the study period. We used the observed numbers of immatures, philopatrics and breeders at the beginning of the time series to define the initial population vectors $N(t = 1)$ and $N(t = 2)$. We then projected the population for 116 time steps using projection matrices $A(t)$ generated with the observed time-series of temperature and food availability. The density covariate was calculated from the projected population size $N(t)$ at every timestep (details in Appendix 2), thus letting population density propagate within the model. We ran one projection using the specific year random effect values estimated by the breeding probability model and another 100 trajectories by sampling this random effect from a normal distribution with the estimated variance. Subsequently, we compared the monthly population numbers predicted by matrix model projections to the observed number of trapped mice in each month.

RANDOM DESIGN LTRE

Population dynamics show responses of varying magnitude to changes in different vital rates and the environmental drivers underlying these changes (Oli, 2004; Coulson *et al.*, 2000). Life Table Response Experiments (LTREs) are retrospective perturbation tools for quantifying relative impacts of matrix elements, vital rates and lower-level covariates on previously observed population dynamics (Caswell, 2001). The dominant right eigenvalues of the matrices (λ) is often used as the response variable of interest in LTREs as it represents long-term population growth rate for density-independent populations in constant environments (Caswell, 2001). Despite this definition not applying here, λ was highly correlated with transient, one-time-step growth rate in our model (Appendix 4: Figures S4.1 & S4.2), and we thus used it as the response variable of an LTRE analysis (for results using

transient one-time-step growth rate instead, see Appendix 3). As we had 116 different matrices available (one for each month of the study period), we used a random design LTRE (Caswell, 2001, chapter 10.2) to decompose temporal variation in λ into contributions from variation in all different vital rates and from the changes in temperature, food availability and population density underlying it. This required sensitivity estimates of λ to changes in environmental covariates, vital rates and matrix elements, and we calculated these numerically using the element-by-element mean of all 116 matrices as a reference (Horvitz *et al.*, 1997). We performed the random design LTRE analysis for all matrices together, as well as pooled into three seasons: breeding season (Aug - Nov), dry season (Dec - Mar) and cold season (Apr - Jul).

QUALITATIVE HINDCAST PERTURBATION

Projections from our matrix model were characterized by population peaks of varying frequency and amplitude (Figure 2). To gain insight into the roles of environmental covariates in producing these patterns in our model, we did a qualitative hindcast perturbation analysis. Specifically, we created 6 hindcast projections in which we disabled the effects of one or two of the environmental drivers by setting them to a constant value, and compared these projections to the unperturbed hindcast. The constant value chosen for all covariates was their mean over the study period, and the random year effect on breeding probability was set to 0 here.

STOCHASTIC DYNAMICS IN A STATIONARY ENVIRONMENT

Stochasticity in environmental conditions is ubiquitous and can strongly influence the dynamics of populations (Tuljapurkar, 2013), particularly in combination with with density-dependence (Boyce *et al.*, 2006; Sæther, 1997). Understanding population dynamics of species like striped mice that inhabit a variable environment and are strongly density-regulated thus requires consideration of environmental stochasticity. We analyzed population dynamics in a stochastic but stationary environment with a prospective perturbation analysis. We generated 10,000 stochastic 200-year time series of temperature and food availability by randomly sampling sequences of the covariates from all years we had data for (2005 - 2014). We defined the year as starting in April, as the population is generally between maximum and minimum densities in this month and each year then contains a distinctive population peak and trough. For each replicate time-series, we then created two perturbed scenarios in which either temperature (S_T) or food availability (S_F) was increased by 1%. We used unperturbed and perturbed environment time-series to simulate future population trajectories, starting the projections using observed population numbers and stage distributions for April 2005. For the stochastic projections, we introduced a maximum litter size threshold of 5.8 (maximum value in the data) to prevent unrealistic behavior of the exponential litter size model.

For each population projection we obtained this way, we determined population size and structure during the population maximum and minimum in each year. Subsequently we calculated the fold-changes of population size and structure, as well as quasi-extinction probability (threshold = 5 females), in scenarios S_T and S_F relative to the unperturbed scenario. Finally, we used additional simulations

in a pathway analysis to determine which vital rates were primarily responsible for the calculated changes in annual minimum/maximum population sizes under scenarios S_T and S_F. We describe this analysis in more detail in Appendix 2.

STOCHASTIC DYNAMICS IN A CHANGING ENVIRONMENT

When studying population responses to climate change, a gradual instead of a constant change in temperature (and potentially other environmental factors) has to be considered (Wolkovich *et al.*, 2014). We explored how stochastic population dynamics of striped mice changed when the population experienced a gradual increase in temperature. The magnitude of this temperature change was inspired by climate change scenarios for South Africa. General Circulation Models predict climate warming in the Succulent Karoo to range from 0.01°C to 0.4°C per year until the end of the century, with the majority of models predicting and increase of 0.02°C to 0.03°C per year (Jury, 2013). We thus assumed an annual temperature increase of 0.025°C for our first climate change scenario ($S_{T\uparrow}$). It is unlikely that the availability of food plants for striped mice will remain unchanged in the future, as rainfall is generally expected to decrease. Climate change scenarios for rainfall in South Africa are very variable and subject to large local differences (MacKellar *et al.*, 2007; Collier *et al.*, 2008), however. This, in combination with direct detrimental effects of increasing temperatures on Karoo vegetation (Musil *et al.*, 2009), makes quantitative predictions of vegetation changes very difficult. We therefore adopted an exploratory approach regarding changes in food availability and included two additional climate change scenarios in which food availability was expected to gradually decrease up to 10% ($S_{T\uparrow F\downarrow}$) or 20% ($S_{T\uparrow F\downarrow\downarrow}$) within 100 years.

For each climate change scenario, we generated 20,000 100-year stochastic environment time series and perturbed them by imposing trends in temperature and food availability as described above. We then ran population projections for 1200 time-steps using the original and perturbed environment time series, and analyzed changes in annual minimum/maximum population sizes and population structures. Contrary to the analyses on stationary environments, we here not only looked at the correlation between the original and perturbed trajectories, but also accounted for temporal changes by fitting a linear model of the form $X_{perturbed} \sim X_{original} + year + year : X_{original}$ where X represents the quantity of interest (population size or structure). For each simulation in each scenario, we used the parameters of this linear model to make an estimate of the fold-change in X after 100 years of exposure to the climate change scenario. The "original" population size and structure we used in those calculations were based on the mean value for the entire unperturbed scenario for each simulation. In a last step, we quantified the contributions of different demographic pathways to changes in annual minimum/maximum population sizes after 100 year exposure to climate change scenarios (details in Appendix 2).

All matrix model analyses were done in R version 3.4.0 (R Core Team, 2015).

Results

MODEL FIT & POPULATION GROWTH RATES

A model hindcast using the observed levels for the random effects in breeding probability performed well at capturing observed population dynamics (Figure 2). The timing of population increases and decreases was well represented by the model,

but peak population sizes tended to be somewhat overestimated. Furthermore, we demonstrated that even when the values of the random year effects on breeding probabilities were sampled randomly, the predicted pattern was well preserved.

We calculated two measures of population growth rate for each of the 116 matrices. The dominant right eigenvalues of the time-specific matrices ranged from 0.82 to 1.6 (mean = 1.01, SD = 0.18). Transient one-time-step growth rates (calculated using both time-specific matrices and observed population structures) took values between 0.81 and 1.95 (mean = 1.06, SD = 0.25). Dominant right eigenvalues and transient growth rate followed the same pattern and were numerically very similar (Appendix 4: Figure S4.1). 93% of variation in transient growth rates was explained by the dominant right eigenvalues of the matrices (Appendix 4: Figure S4.2).

RELATIVE STRENGTHS OF DRIVERS OF PAST POPULATION CHANGE

Decomposition of variation in the dominant right eigenvalues of the matrices using a random design LTRE identified food availability, working primarily through litter size, as the main driver of past population changes. The contribution of changes in food availability was 0.021, and thus three times as large as the next influential quantity, variation in population density (contribution = 0.007). Contributions from variation in temperature and covariation among different environmental factors were comparatively small (Figure 3). Among vital rates, the strongest contribution came from variation in litter size (0.008), followed by variation in philopatric maturation probability (0.005, Appendix 4: Figure S4.4). Other considerable contributions came from variation in breeding probability and litter probability, as

well as their covariances with each other and with philopatric maturation probability. These relative rankings were conserved when variation in transient growth rate (instead of dominant right eigenvalue) was the quantity of interest (Appendix 3).

Seasonal analysis revealed that food availability only had the largest contributions in the breeding and the cold season. In the dry season, the largest contribution was ascribed to population density (Appendix 4, Figure S4.3). Similarly, contributions from philopatric maturation probability were more important than contributions from litter size in the dry season only (Appendix 4, Figure S4.5).

QUALITATIVE PERTURBATION OF POPULATION HINDCASTS

Excluding temporal variation in environmental covariates led to different changes in population dynamics (Figure 4). Removing temperature variation resulted in only slight changes in the height of population peaks. When the effect of food availability was ignored, on the other hand, both population increases and decreases were lost almost completely, irrespective of whether or not temperature was allowed to vary. Finally, disabling the density feedback led to rapid population explosion. Again, this was the case both with varying and constant temperature. Disabling the density feedback in the presence of constant food availability resulted in a population that was almost constant at a small size, and showed only low amplitude fluctuations as a consequence of varying temperature.

STOCHASTIC DYNAMICS

Population trajectories obtained for stochastic environments were characterized by marked differences in peak population sizes (Appendix 4: Figure S4.6), but

every peak was followed by a similar crash. This behavior led to perturbed trajectories that differed from original trajectories in minimum and maximum annual population sizes, but did not diverge strongly from original trajectories over time (Appendix 4: Figure S4.7).

Population peaks in stationary environments became higher when either temperature (mean fold-change = 1.009) or food availability (mean fold-change = 1.025) was increased by 1% (Figure 5a & b). In both perturbations, these increases were primarily driven by changes in litter size and the maturation probability of immatures (Figure 5c & d). Minimum population sizes became larger under increased food availability (mean corr. coefficient = 1.005) due to changes in litter probability, breeding probability and philopatric maturation probability. Increased temperature, on the other hand, could lead to either smaller or larger minimum population sizes depending on the stochastic sequence of years, and contributions were spread over several vital rates (Figure 5b & d). Perturbations also affected population structure: during population peaks and lows, higher temperature led to a larger proportion of philopatrics, while higher food availability resulted in more philopatrics and breeders (Appendix 4: Table S4.1). Extinction probability over the simulated 200-year period was small at 5.2% for unperturbed trajectories, but decreased further to 4.8% and 4.9% when temperature and food availability were increased.

Annual maximum and minimum population sizes displayed distinct responses to different climate change scenarios (Figure 6a & b). With gradually increasing temperature but no change in food availability ($S_{T\uparrow}$), peak population sizes increased by 11.2%, while minimum population sizes decreased by 2.6% on average over a 100-year period. This positive effect of increasing temperature on

peak population sizes was offset if accompanied by a 10 % gradual decrease in food availability ($S_{T\uparrow F\downarrow}$): Maximum population size after 100 years was lower in all simulations, with an average decrease of 10.1%. Minimum population size decreased by an average of 4.2%, although increases were seen in some simulations (Figure 6b). When food availability decreased even more (20% in $S_{T\uparrow F\downarrow\downarrow}$), maximum population size decreased by 29.6% and minimum population size by 12.7% on average. Decreases in minimum population sizes were driven by changes in maturation, breeding and litter probabilities. The same vital rates were responsible for lower peak population sizes under $S_{T\uparrow F\downarrow}$ and $S_{T\uparrow F\downarrow\downarrow}$, while the higher population peaks under $S_{T\uparrow}$) were primarily due to changes in litter size.

Stage structure during the maximum and minimum population sizes was affected similarly by all three climate changes scenarios: Populations had a considerably higher proportion of philopatrics and lower proportion of breeders after 100 years of exposure to the scenarios (Appendix 4: Figure S4.8 & Table S4.2). The proportion of immatures on the other hand decreased only when food availability was projected to go down ($S_{T\uparrow F\downarrow}$ & $S_{T\uparrow F\downarrow\downarrow}$) and showed very variable responses when only temperature increased ($S_{T\uparrow}$).

Extinction probability was almost halved when temperature increased gradually (decrease from 2.6% without perturbation to 1.4% under $S_{T\uparrow}$, fold decrease = 1.83). An accompanying moderate decrease in food availability ($S_{T\uparrow F\downarrow}$) resulted in a 1.29-fold decrease in extinction probability (2.6 to 2.0%), whereas with a higher food decrease ($S_{T\uparrow F\downarrow\downarrow}$), it increased 1.45-fold (2.6 to 3.8%).

Discussion

In this study, we analysed population dynamics of a small semi-desert rodent on multiple temporal scales ranging from short-term month-by-month changes to long-term projections spanning several decades. By explicitly including environment-demography relationships, we obtained a population model able to reproduce past population dynamics and identified food availability affecting reproduction and resulting density feedbacks as the main mechanisms driving the strongly fluctuating population dynamics of our study species.

Analysing the population dynamics on short timescales, we found that variation in monthly population growth rates was mainly due to changes in food availability (Figure 3) affecting vital rates linked to reproduction (predominantly litter size, Appendix 4: Figure S4.4). The same general pattern emerged for multi-annual stochastic population dynamics: elevating food availability resulted in larger population sizes during annual peak and low phases as a result of changes in maturation rates and reproductive output (Figure 5). The importance of food availability was emphasized further by the fact that population fluctuations largely disappeared when variation in plant cover was ignored (Figure 4). These findings are consistent with other studies that found food availability to be the main driver of population fluctuations of rodents in semi-arid environments (Brown & Ernest, 2002; Previtali *et al.*, 2010; Lima *et al.*, 2008), as well as primary consumers in general (Hunter & Price, 1992; Kagata & Ohgushi, 2006). In the case of striped mice, opportunistic breeders displaying a high degree of plasticity in reproductive timing (Raynaud & Schradin, 2008; Nel *et al.*, 2015), the population increases following elevated food availability are likely the results of prolonged reproductive

seasons with many young animals starting to breed early, potentially followed by "out-of-season" reproduction due to more favorable conditions.

The second-most important driver of changes in monthly population growth rates was population density (Figure 3). Variation in population growth rates during months with scarce food (dry season) was even primarily due to changes in population density (Appendix 4: Figure S4.3). Stronger density feedbacks when populations are close to their carrying capacity (*e.g.* due to resource scarcity) have been found in a range of species including other rodents (Goswami *et al.*, 2011), ungulates (Albon *et al.*, 2000; Coulson *et al.*, 2001), and raptors (Krüger, 2007). This reflects the importance of population density in regulating and stabilizing population dynamics (Hanski, 1990), and is further supported by our model predicting either rapid population explosion or extinction when the density feedback was disabled (Figure 4). The impacts of density feedbacks were very evident in multi-annual population dynamics as well: While both increases in food availability or temperature led to larger annual minimum and maximum population sizes (Figure 5a & b), these changes did not add up over time and populations in perturbed environments did not progressively diverge from those in unperturbed environments (Appendix 4: Figure 4.7). This indicates that density regulation is strong enough to "reset" population dynamics every year, and supports the hypothesis that strong density feedbacks buffer populations of fast-living species against environmental change (Williams, 2013).

Temperature only explained a small fraction ($\approx 4\%$) of the variation in short-term population growth rates (Figures 3) and increasing it led to smaller changes in long-term population abundances than increasing food availability (Figures 5). This is a result of relatively weaker impacts of temperature on vital rates (Nater

et al., 2016a), and may be partially related to the generally lower interannual variation in temperature relative to food availability and population density.

Long-term population responses of striped mice under climate change scenarios depended strongly on the assumed change in food availability. Rising temperatures alone resulted in larger annual population peaks as a consequence of increased litter size (particularly outside the main breeding season), and variable responses of annual minimum population size (Figure 6). Adding a gradual decrease in food availability, however, led to reduced maturation, breeding and litter probabilities, and ultimately populations with overall lower abundance (minimum and maximum population sizes, Figure 6). The strength of this response scaled with the magnitude of the food decline. This lower reproductive output during the main breeding season led to lower peak densities, which in turn let more philopatrics survive the dry season and thus contribute to the following minimum population size. This is supported by the generally higher percentage of philopatrics in populations experiencing climate change (Appendix 4: Figure S4.8). Striped mice are known to delay reproduction, likely to increase their chances of surviving the harsh dry season and then breed the following spring (Schradin *et al.*, 2012). Our analyses indicate that under harsher conditions (*e.g.* increasing temperatures and decreasing food availability associated with climate change), more mice may be forced to adopt this strategy, and possibly for a longer period of time. Delayed maturity under adverse environmental conditions has been studied in long-lived species (*e.g.* seabirds, Nevoux *et al.* (2010)), but less in short-lived species, making the striped mouse an interesting system for future study of the role of delayed reproduction in mediating environmental change.

The quasi-extinction probability of striped mouse populations over 100 years

increased only under the scenario with the strong decrease in food availability ($S_{T\uparrow F\downarrow\downarrow}$), and even then was still quite low at 3.8%. This too is related to the strong density feedback stabilizing the population and thus buffering it even against large changes in the environment. Under the investigated scenarios, our simulations thus do not indicate that gradual climate change threatens persistence of striped mice in the Succulent Karoo. However, the climate change scenarios we used here may be only partially representative of future environmental change, and future studies could improve on this from two perspectives.

First, the simulated decreases in vegetation cover were only qualitatively linked to predicted future changes in rainfall and scenarios may therefore not accurately represent the expected change in food availability due to climate change. Having a model linking vital rates directly to food availability - instead of indirectly through rainfall as done in many other studies on arid ecosystems (*e.g.* Ozgul *et al.*, 2014) - granted us more insight into the biological mechanisms underlying population dynamics. However, the downside of this is that in order to run this model under more realistic climate change scenarios, the relationship between rainfall and vegetation cover needs to be quantified. This is a non-trivial task, as vegetation responds to rainfall in a complex and non-linear way, depending not only on amount but also timing of rainfall (*e.g.* 100mm of rain over the course of a month stimulating plant growth vs. 100mm of rain falling within one day and destroying vegetation). Second, climate change will not only lead to gradual changes in mean environmental variables, but also increases in the frequency of extreme weather events (IPCC, 2014). We have not considered such events in the current study, but they can potentially have strong impacts on population dynamics (van de Pol *et al.*, 2010). In semi-arid Chile, for example, extreme flooding events following

catastrophic rainfalls can reset long-term demographic trends and community dynamics (Kelt, 2011), and similar flooding events can occur in the Succulent Karoo with potentially detrimental consequences for striped mice. Extreme events also happen in the form of droughts and temperature anomalies, such as in the unusually dry winter of 2003 which wiped out almost our entire study population (pers. observation). So while the results from this study indicate that moderate trends in average temperature and food availability do not threaten viability of striped mouse populations, the same may not be true for changes in frequency and intensity of extreme weather events. Quantifying the general relationship between vegetation cover and rainfall, as well as occurrence and consequences of extreme events (*e.g.* floods, droughts), are thus important topics for future research and will allow us to make more realistic predictions of striped mouse population responses to climate change.

Another area to improve on is the accuracy of numerical predictions. While our population model produced a good fit to observed data, achieving this numerical accuracy required adjustment of litter size estimates using auxiliary information. The original measure of litter size had been consistently too low due to a combination of low detectability of immatures and potential overestimation of the number of breeding females (Appendix 1, Section 1.2). In order to obtain more accurate numerical predictions, future studies should aim to quantify litter size more precisely. This could be done, for example, by using open population mark-recapture designs to account for the low detectability of immatures (Pradel, 1996), larger-scale genetic studies (sensu Schradin *et al.* (2012)) to reliably identify the females giving birth and their offspring, and experiments investigating the environmental effects on both the actual number of pups born to a female as well as nest survival

of those pups.

Lastly, and particularly when discussing responses to climate change, one has to keep in mind that in this study, we have considered only a single population of striped mice in isolation, ignoring immigration and spatial dynamics and accounting for predation only indirectly (through survival estimates, Nater *et al.* (2016a)). However, interactions and movement between different striped mouse populations are likely important, and so is the general role of striped mice in the foodweb. In (semi-)arid environments, small mammals often have important roles as keystone (prey) species and ecological engineers (Kelt, 2011). If climate change reduced overall abundance of striped mice (and potentially other rodent species) - as predicted in this study - this could have cascading effects on the abundance of bird, reptile, and carnivore predators (Byrom *et al.*, 2014), on the spread of invasive species (Madrigal *et al.*, 2011), and on the plant species richness that makes the Succulent Karoo a unique biodiversity hotspot (Hillebrand *et al.*, 2007). Such effects on other trophic levels could, in turn, feed back again on rodent (meta-)population dynamics. To make realistic predictions on how the Succulent Karoo as a whole (and similar biomes) will respond to climate change, an ecosystem approach coupling climate to plant, rodent and predator populations and including feedbacks between the different trophic levels will therefore be invaluable.

Environmental factors and density feedbacks have long been recognized as the key determinants of population dynamics, and studying these relationships via variation in vital rates has emerged as a powerful approach (Gamelon *et al.*, 2017). Nonetheless, environmental factors are rarely included into population models explicitly and few models consider interactions between the extrinsic environment

and density feedbacks (Ehrlén *et al.*, 2016). In this study, we have accounted for these complexities by building a density-dependent population model based on estimated environment-vital rate relationships. Using this model, we have shown that both short- and long-term population fluctuations of a semi-desert rodent are sensitive to changes in food availability affecting reproduction, but also strongly mediated by intrinsic feedbacks. Strong density dependence thus buffers this population against environmental change, and the environmentally explicit population model enabled us to gain unique insights into the demographic mechanisms underlying this buffering.

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Author's contributions

CN, KB, CC, CS and AO conceived the ideas and designed methodology. CS collected the data. CN and KB analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data available from the Dryad Digital Repository: `https://doi.org/10.5061/dryad.c1657.2` (Nater *et al.*, 2016b).

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Supporting information

The following Supporting Information is available for this article online: Appendices 1-4.

Figures

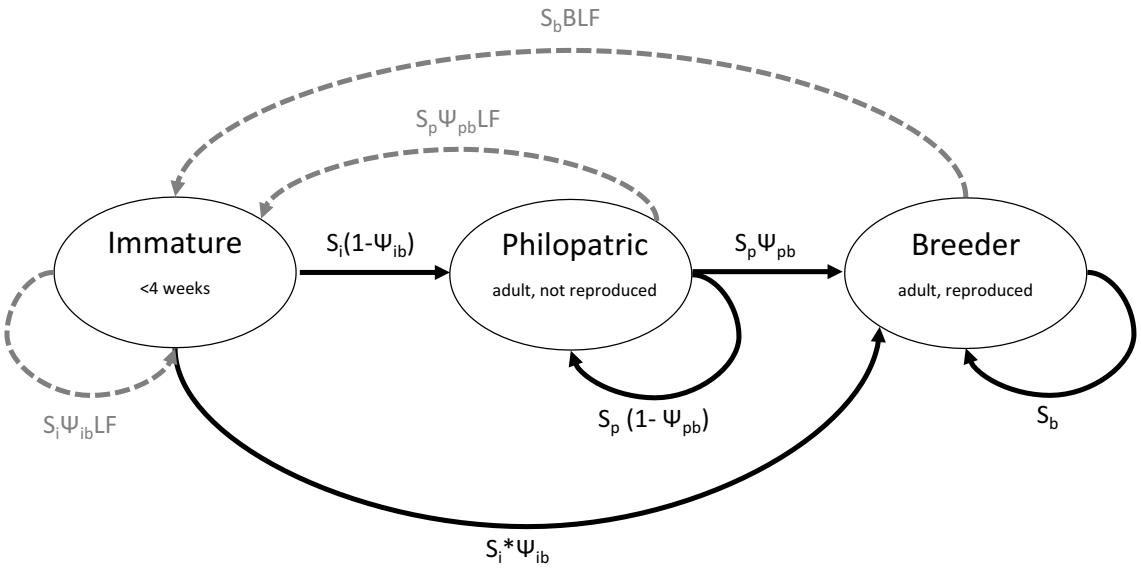

Figure 1: Life cycle of the African striped mouse (post-breeding census). S indicates survival probabilities, Ψ maturation probabilities, B the breeding probability, L the litter probability, and and F the litter size. Subscripts for life stages: i = immature, p = philopatric, b = breeder).

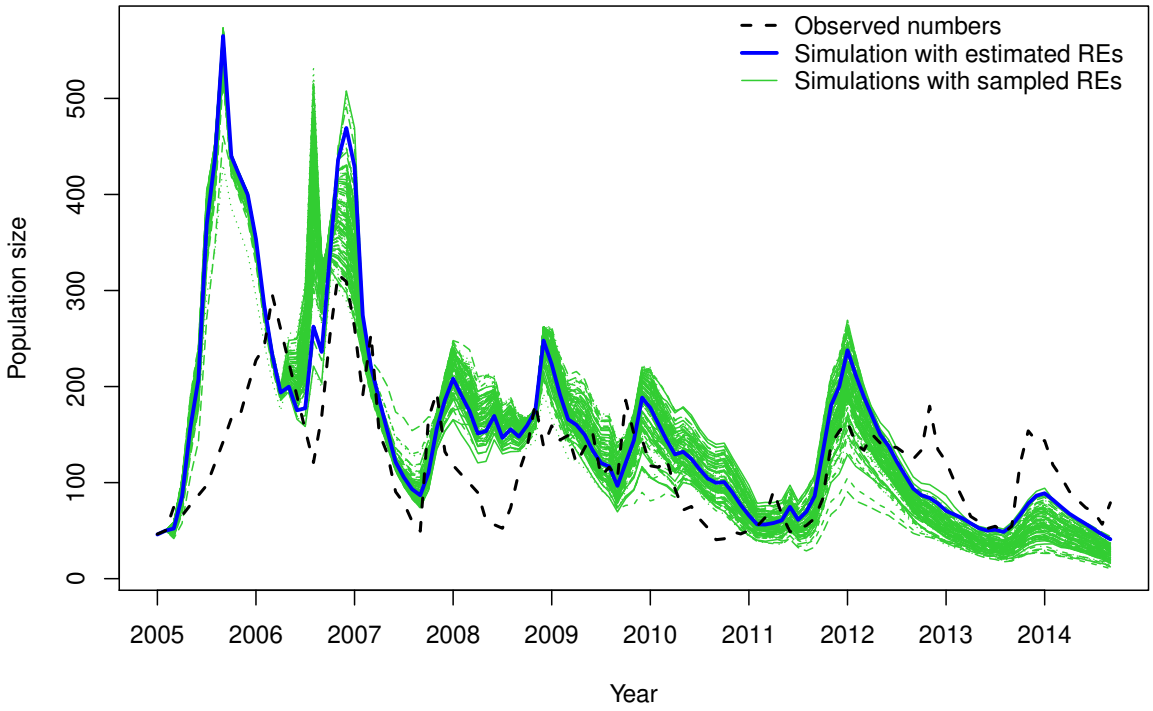

Figure 2: Observed population sizes (black, dashed), model projections using observed levels of random variation (blue), and 100 model projections where random effects were sampled from a normal distribution (green).

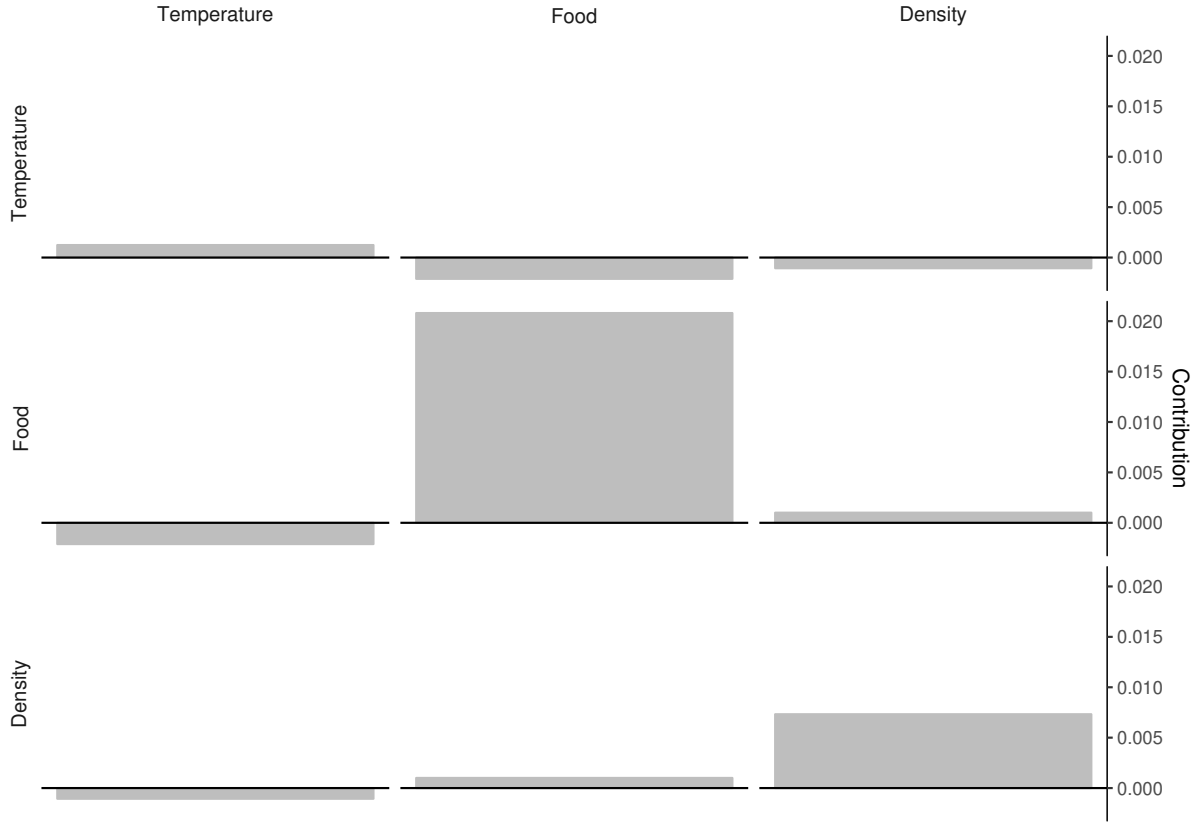

Figure 3: Relative contributions of variances and covariances of temperature, food availability, and population density to variation in the dominant right eigenvalue λ.

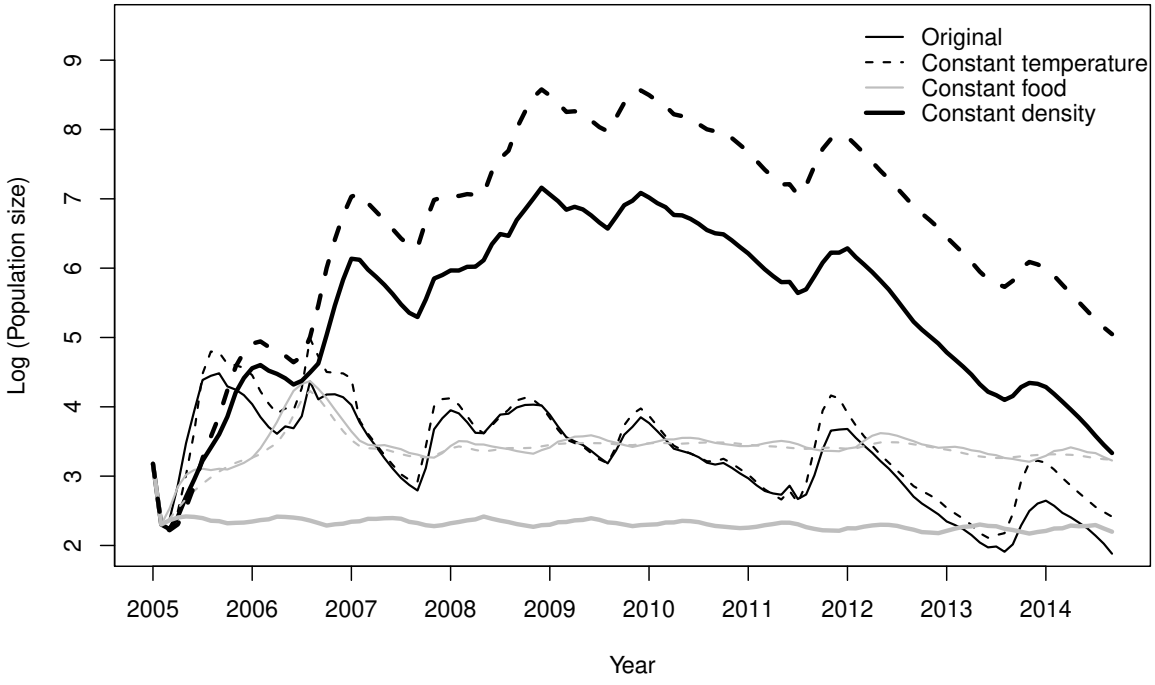

Figure 4: Original and perturbed model hindcasts, where one or two environmental covariates are set to be constant at their mean value. Dashed lines have constant temperature, grey lines have constant food availability, and thick lines have constant density (disabled feedback).

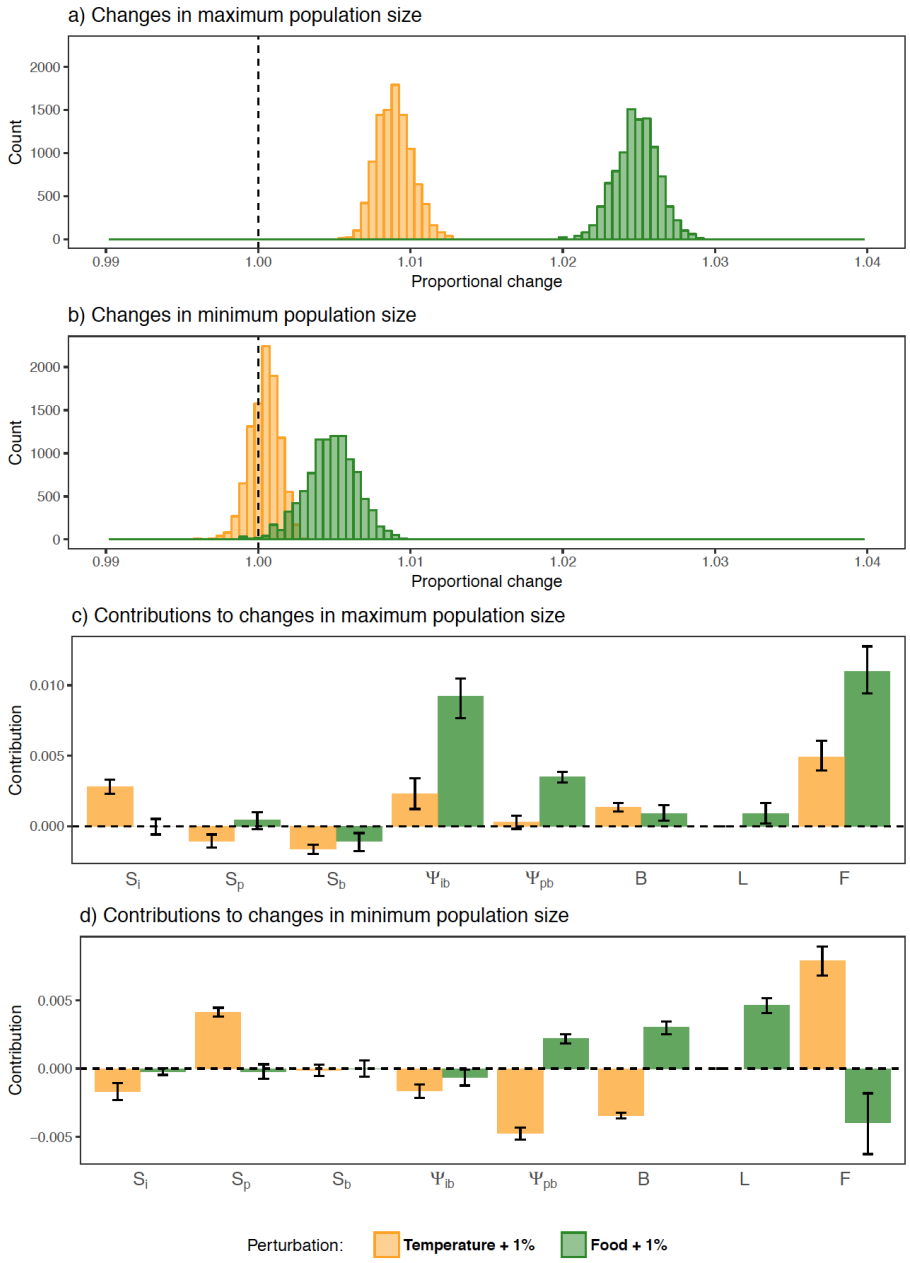

Figure 5: Panels a) and b) show the distributions of proportional change in maximum and minimum population sizes over 200 years when either temperature (orange) or food availability (green) was increased by 1%. Panels c) and d) show the relative contributions of different demographic pathways to those changes. Colored bars represent mean values, black margins mark the 95% confidence interval. Estimates of both population size change and vital rate contributions are based on 10,000 replicates for each scenario.

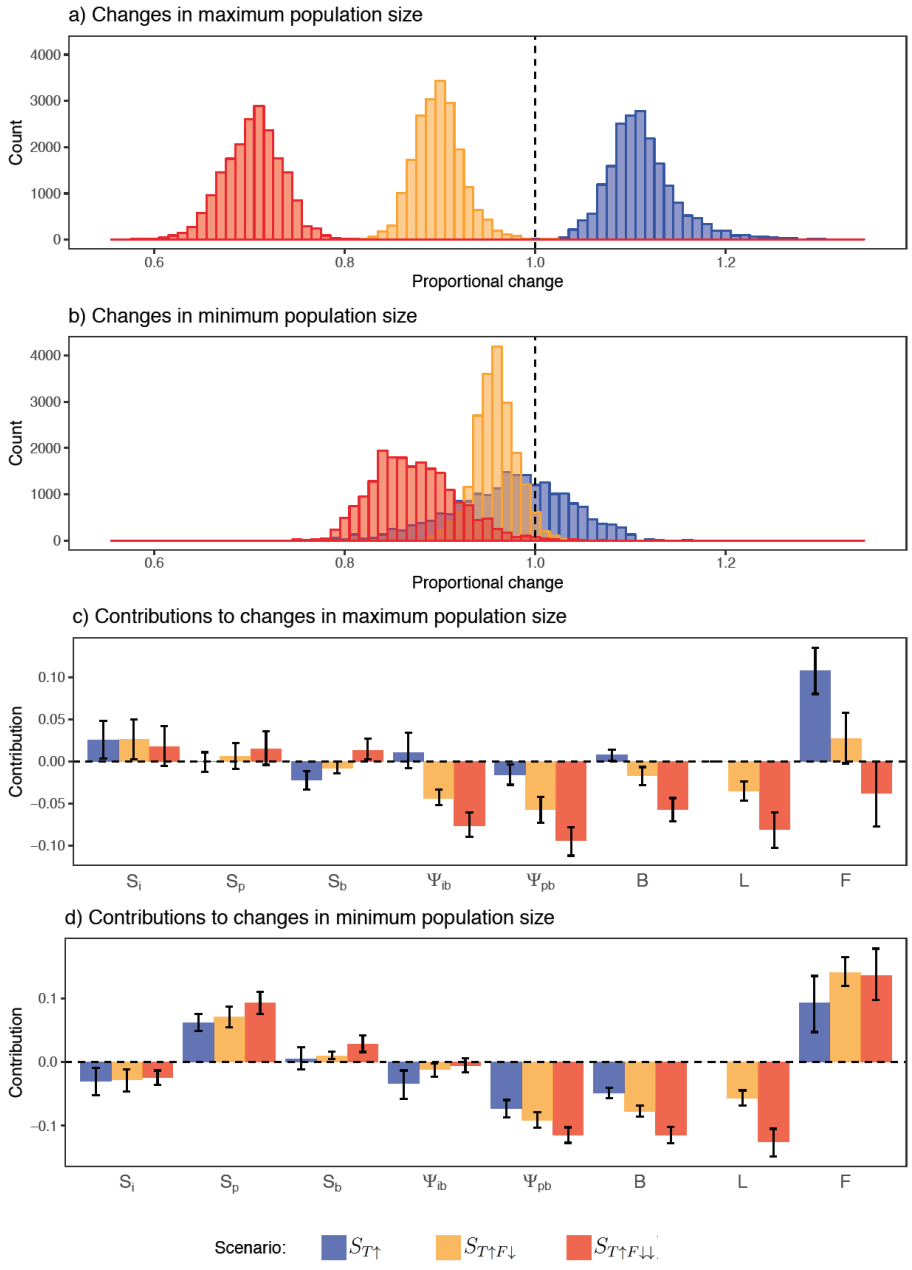

Figure 6: Panels a) and b) show the distributions of proportional change in maximum and minimum population size after a 100-year projection under the three climate change scenarios. Panels c) and d) show the relative contributions of different demographic pathways to those changes. Colored bars represent mean values, black margins mark the 95% confidence interval. Estimates of both population size change and vital rate contributions are based on 20,000 replicates for each scenario.